SOME REMARKS ON THE ROLE OF THE SOIL IN THE EVOLUTION OF EARLY ANTENNATA

W.Dunger
Staatliches Museum für Naturkunde, Görlitz, DDR

НЕКОТОРЫЕ ЗАМЕЧАНИЯ О РОЛИ ПОЧВЫ В ЭВОЛЮЦИИ РАННИХ АНТЕННАТ

В.Дунгер
Государственный музей естественной истории, Гёрлитц, ГДР

To commemorate the world-famous soil zoologist Professor M.S.Ghilarov, this short account reviews ideas on the possible significance of soils in the evolution of early Antennata. As early as in /5/, Professor Ghilarov had put forward a theory about the soil as an ecological factor in the transition of invertebrates from aquatic to a terrestrial way of life.

The modern knowledge of early Antennata is mainly based on fossil records from three Devonian localities: Rhynie (Scotland), Alken an der Mosel (Federal Republic Germany), and Gilboa (New York) /13,14/. Although the fossil material is sparse, its diversity is astonishing. It shows that most of the main groups of terrestrial arthropods are not only represented but highly specialized in the early Devonian. The earliest relative of the Carboniferous genus Arthropleura is Eoarthropleura devonica from Alken /16/. The oldest fossils of centipedes (from Gilboa) are a complete first trunk appendage with poison claws very similar to the Recent genus Craterostigmus as well as fragments of legs and tergits that may belong to a member of the order Scutigeromorpha /14/. The oldest Collembola, Rhyniella praecursor from Rhynie, is perhaps near to the Recent family Neanuridae (that is called into question after restudy by P.Greenslade; pers. comm. August, 1985) and already highly specialized /11,18/. A head fragment with a compound eye and parts of terga from Gilboa are supposed to belong to a Machilid. If we disregard milliped-like remains of Ludlow time /12/, the oldest true millipeds appear in the Scottish Old Red Sandstone which is now considered to be Silurian rather than Devonian. Besides Antennata, there are found aquatic scorpions, spiders and mites in the mentioned localities.

During much of the Devonian, the three sites were relatively near to each other in the equatorial region on the Laurussian Plate, with a tropical palaeoclimate. The environmental conditions are supposed to be deltas, lagoons and channels flanked by a kind of land vegetation, or swamps. The predominant terrestrial substrate is thought to be fine grained and compact layered aggregates of minerals, i.e. uncemented rock.

Early land plants appear also in the Silurian, but records of well represented vascular plants at least in restricted areas, are not known until the Devonian. For the first step of land invasion by the early Antennata the Silurian pioneer vegetation of nonvascular thalloid land plants, algae, fungi and bacteria, seems to be more important. In /7/ it was demonstrated that during the early Devonian the morphology and sculpture of spores show increasing diversity and explain this phenomenon as a reaction against arthropod feeding. Faecal pellets with fungal hyphae were found in the Swedish Ludlow /15/, possibly from springtails, mites or millipeds. In /13/ this is mentioned as evidence of early occupation of the terrestrial decomposer niche and takes it as a proof of existence of soils, by then. At favourable sites there may even have been a development of some kind of raw soil with a superficial layer of arthropod pellets, very susceptible to desiccation. Such "soils" lacked roots and substrate mixing animals and therefore had no organic material in the deeper layers. Even comparision with Recent soil formations on dunes or rocks is not fully applicable because of the lack of air-drifted organic material in the Silurian.

The results of paleontology may be summed up as follows: development and early differentiation of the Antennata had occurred by the Silurian. This must be taken into consideration when reconstructing the palaeoecology. The environment of early Antennata is likely to have been temporary swards of microphyta and thalloid plants upon raw soil-like substrates. Soils with a highly developed structure, such as presumed by Ghilarov in /6/ for the transition of life from water to land, should not be expected until perhaps the Carboniferous.

Another approach to understanding the evolution of early Antennata is provided by comparative morphology and physiology. Arthropods undergo five essential adaptations to terrestrial life /16/. Locomotion, the function of sense organs, respiration and protection against desiccation may be preadapted in the Proantennata. Newly gained properties are adaptations for the uptake of dry food, especially the formation of a preoral cavity, as well as organs for excretion under terrestrial dry conditions. These adaptations are gained convergently by Antennata and Chelicerata. Phylogenetic systematics have paid much attention to these processes. The supposed role of the ecological situation, especially of the soils in the transition to a terrestrial way of life have had much influence upon attempted reconstructions of the phylogeny of terrestrial arthropods. Phylogenetic relationships of the Recent classes of Antennata have been differently interpreted. From the basic Antennatan stock have branched off probably /1,3/ first the Chilopoda, second the Insecta, third the Symphyla and lastly the Dignatha (Pauropoda and Diplopoda). If that is true, all classes of Antennata must have been differentiated by the Silurian.

Opinions on the role of soils as a habitat for the first steps of evolution have had a decisive influence on theories about the phylogeny of the Chilopoda. Many authors /9 a.o./ considered the adaptation of the Geophilomorpha to life in soil interiors to be primary, and all other Chilopoda up to the Scutigeromorpha to be descended from Geophilus-like predecessors. In contrast, phylogenetic systematics /2 a.o./ comes to the conclusion that the Scutigeromorpha are the most basal Recent class of the centipedes. Most probably the Prochilopoda were hunters upon the terrestrial surface. Inside the Silurian soil-like substrate they could probably neither move nor feed. As a prey one may imagine perhaps amphibious Proantennata. Fossil records of the last years seem to corroborate this hypothesis /14/.

Earliest insects, which first made the transition to a hexapodous locomotion, differed from Recent Apterygota. Nevertheless, Collembola must have arisen very early from this stock, as is demonstrated by the Devonian genus *Rhyniella*. The early springtails, too, may not have been dwellers in the interior of Silurian "soils". One of the characteristic features of Collembola is the transformation of functionless abdominal legs into a jumping organ (furca), doubtless a reaction to predators. Inside the soil the furca is completely useless. The primary Collembola may have grazed upon Silurian swards of Microphyta and its detritus. Moreover, they were successful in avoiding predation by jumping. The development of the main branches of Collembola probably occurred in the Silurian. It is only secondarily that euedaphic life-forms arose convergently within different groups of Collembola, in connection with the increasing formation of the soils. Extremely adapted euedaphic genera like *Tullbergia* s.l. belong to the youngest taxa of springtails.

The Diplopoda are characterized by the possession of diplosegments. On the hypothesis of the primary role of soils as well as from experimental evidence, the formation of diplosegments in earliest Diplopoda is explained as a mechanical necessity in order to push the body head-on through the soil. This implies that the first millipedes must have been dwellers in the interior of "soils". Even if one suppose that these animals bored into the substrate only for moulting and to avoid desiccation, this argument is not convincing. Among other things, it cannot explain the undoubted tendency to the formation of bisegment-units in the other classes of Myriapoda, especially in the Pauropoda. Above all it is applicable only to millipeds with solid body rings, that is for the "bulldozer type", occurring in Juliformia and Merocheta. It is just these orders that are considered by phylogenetic systematics to be the highest developed branches of Diplopoda /4,3/ and which are not imaginable as basic millipeds. The oldest true millipeds from the Lower Red Sandstone (Scotland, Upper Silurian), e.g. *Kampecaris forfarensis*, usually have no calcified cuticle /12/. Paleontologists suppose it to be caused by pre-moult autolysis or diagenesis. It is, however, possible that early Diplopoda had naturally no distinctly marked calcification as is the case with the recent dwarfish Pselaphognatha. In all possibility the earliest Diplopoda may have grazed like Collembola or the recent milliped genus *Polyxenus* as cryptobiotic decomposers on algae, bacteria, fungi or thalloid plants in the Upper Silurian and/or Lower Devonian, avoiding predation otherwise than Collembola by different kinds of integument sculpture. Later they may have climbed on vascular plants as suggested by fossils of huge species with large eyes and bifurcated spines. It is suggested /8/ that competition with or opponence of evolving insect groups accounts for diplopod's invading soils which were progressively forming at that time. It was the subsequent change of habitat that induced the formation of more rigid body rings.

An unexpected evidence for an epiphytic stage of Diplopoda was found by /17/. Within guts of Recent millipeds they discovered a new characteristic group of Actinomycetes (*Promicromonospora*) related to old epiphytic groups. This enterosymbiosis may be the result of coevolution between these Actinomycetes and their hosts which started in the "epiphytic time" of Diplopoda.

Altogether there is only one possible conclusion: If we abandon Manton's mechanical hypothesis for the formation of diplosegments, palaeontological data and the main lines of phylogenetic systematics agree.

Summing up, we see that fossil records of recent years have shifted the time of early development of Antennata into the Silurian. The hypothesis about the ecological conditions and the significance of possible soils for the evolution process in Antennata must therefore be revised. Coevolution of land plants and terrestrial arthropods has surely influenced the formation of soils since the Devonian. We have to expect that the essential steps in the evolution of true soil arthropods will be correlated with the increasing differentiation of soils in the Carboniferous.

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Discussion

Golovatch S.I.: You certainly know the recent works by Hannibal, Shear etc. on the Devonian of Gilboa, where good remains of Crateraspis-like chilopods as well as of Collembola have been found. This confirms the idea of a highly early (Silurian?) differentiation of Antennata.
Have I understood correctly that you said the diplopodan "Körperbildung" is designed for soil dwelling?
Your work looks quite compilative, does it not?
Dunger W.: First I must insist that my point is the possible role of "soils" in Antennatan evolution. As to the Ist question, I agree. What about the second question - you have answered yourself in your papers, I agree too. The 3-rd question I could like to give back to you. Surely we agree that compilation in comparing the results of different readings may not be useless. The question: Do then arise any conclusions from studying phylogenetic dendrogramms of Diplopoda and thinking about the proportions of epigeic, semi- or euedaphic forms in different orders?
Dunger W.: Surely there are no strong correlations because of the many adaptive lines that have been shown actually by Dr. Golovač. But seeing it in a very overall view, most of the euedaphic life-forms you can find in the Juloid Diplopoda.
Striganova B.R.: If Antennata appeared in Silurian, are they, according to your hypothesis, related to primary soils,which in that epoch possibly developed under the influence of Cyanophyta and other microorganisms. What could be their terrestrial habitats?
Dunger W.: Early Antennata must be both consumers of microorganisms and thalloid plants and predators on other early arthropods. This complex must have cooperated in forming the first soil life substrates in terrestrial conditions.